Larval Development of the Megabalanine Balanomorph *Megabalanus rosa* (Pilsbry) (Cirripedia, Balanidae)

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CHOI, K. H., ANDERSON, D. T., & KIM, C. H. Larval development of the megabalanine balanomorph *Megabalanus rosa* (Pilsbry) (Cirripedia, Balanidae). *Proc. Linn. Soc. N.S.W.* 113 (3), 1992: 175-184.

The larvae of *Megabalanus rosa* were reared in the laboratory. Naupliar development is planktotrophic, reaching the cyprid stage in 14-16 days at 20°C. Diagnostic features of the stages, including limb setation, are described. The relatively large nauplii, with a smooth, globular dorsal shield, resemble those of *M. tintinnabulum*, but differ from the spinose larvae of *Austromegabalanus nigrescens*. Larval evidence is used to discuss interrelationships of three megabalanine genera.

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INTRODUCTION

Megabalanus rosa (Pilsbry, 1916) has a relatively limited geographical range in the northwest Pacific, being found in the inshore waters of Korea, Japan and Taiwan, with a depth range from the lower littoral to 300 m (Newman and Ross, 1976; Kim, 1985). The species is prominent among the lower littoral fauna of the Korea Strait and East China Sea. Fouling has led to the sporadic spread of *M. rosa* to port waters in other localities such as eastern and western Australia (Jones *et al.*, 1990).

The larval development of *M. rosa* has not been described. Among the megabalanine Balanidae, larval development is known for only one species of the warm water genus *Megabalanus*, *M. tintinnabulum*, and two austral species, *Notomegabalanus agricola* and *Austromegabalanus nigrescens* (Sandison, 1954; Daniel, 1958; Egan and Anderson, 1987). On the basis of this limited evidence, each genus has a distinctive pattern of larval development (Egan and Anderson, 1987), but the account by Daniel (1958) for *M. tintinnabulum* indicates that development in this widespread species is specialized in a number of ways (e.g. very rapid succession of non-feeding naupliar stages; unusually large cyprid) and may not be typical of other species of *Megabalanus*. The present work provides an opportunity to test this question and to extend the comparison of larval development in the megabalanines.

MATERIALS AND METHODS

Megabalanus rosa was collected from rocks and bivalve shells (*Mytilus coruscus*) of the lower littoral of Kadǒck Island, Kyǒngsangnam-do, South Korea. Adults were maintained in the laboratory at 20°C in filtered sea water and fed on *Artemia* nauplii. Release of larvae was observed in February, 1988. Adults were then opened to obtain egg lamellae containing late stage embryos. When transferred to filtered sea water, these lamellae provided a source of newly hatched larvae (Egan and Anderson, 1985).

Some larvae were fixed immediately after hatching. Others were transferred to bowls of filtered sea water at 20°C and fed on *Nitzschia closterium*. Development through six naupliar stages to the cyprid took 14-16 days. Exuviae and specimens of each developmental stage were fixed in 5% neutral formalin.

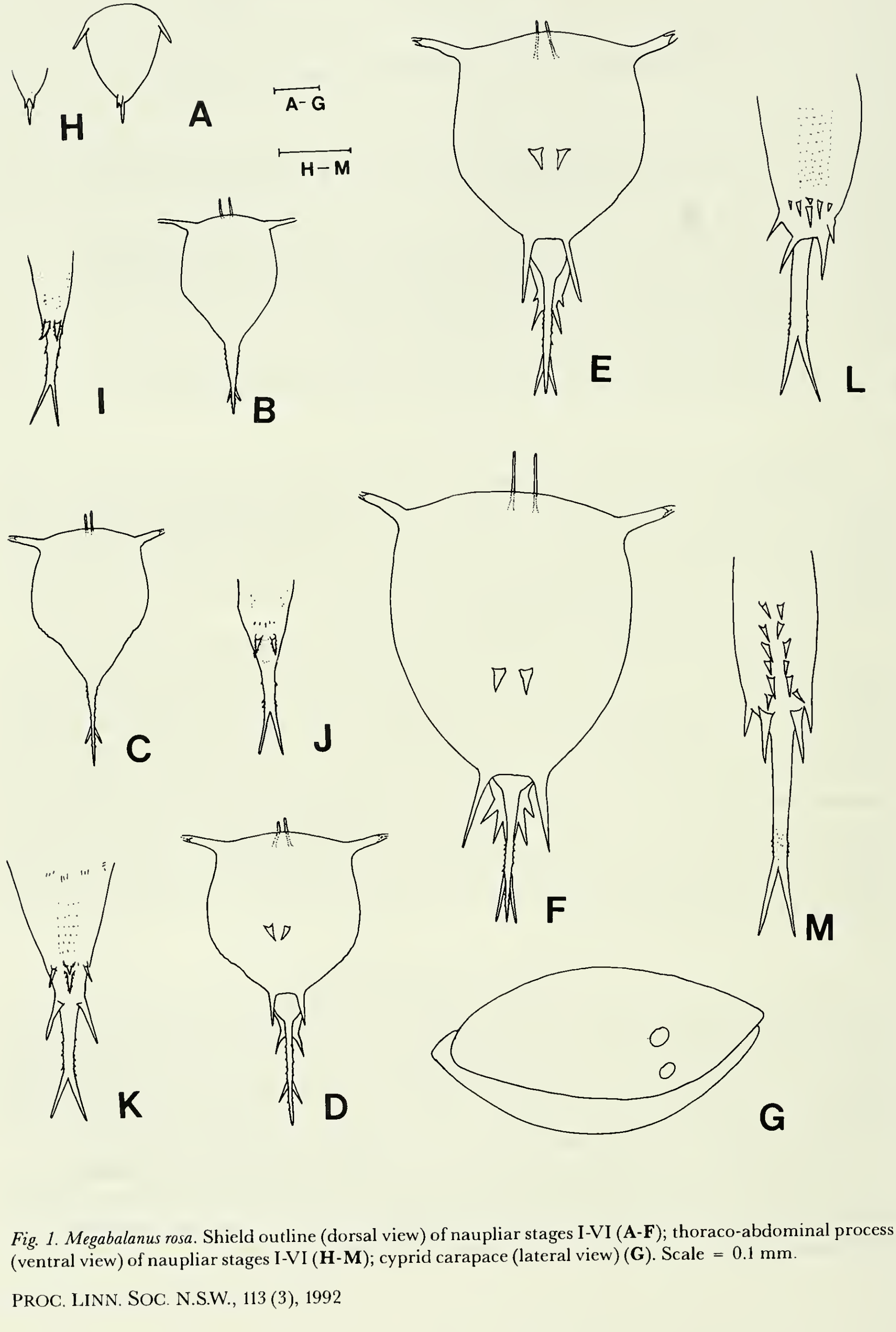

Fig. 1. Megabalanus rosa. Shield outline (dorsal view) of naupliar stages I-VI (**A-F**); thoraco-abdominal process (ventral view) of naupliar stages I-VI (**H-M**); cyprid carapace (lateral view) (**G**). Scale = 0.1 mm.

At least ten specimens of each developmental stage were examined by dissection in a mixture of 70% ethanol:30% glycerine, using fine needles. Either 1% Methyl Blue or 1% Gentian Violet were used for staining. Drawings were prepared using a camera lucida. The developmental stages were distinguished according to the system of Lang (1979). The setal formula and terminology applied to each stage were those of Bassindale (1936) and Branscomb and Vedder (1982).

RESULTS

Larval Morphology

The mean sizes of the larval stages are given in Table 1 and the nauplii are illustrated in Figs 1 and 2. The nauplii of *M. rosa* are relatively large and globular. The body length from the anterior shield margin to the tip of the dorsal thoracic spine is only 1.65-2.0 times the width of the shield. The frontolateral horns are of moderate length, showing a relative increase in length and a development of simple terminal spination in stages IV-VI. The shield margin is smooth in all stages. A single pair of dorsal shield spines is prominent in stages IV-VI, together with a pair of long, smooth posterior shield spines. The dorsal thoracic spine and thoraco-abdominal process are weakly barbed. Furcal spines are typically balanid. The tip of the labrum is square in outline, with a prominent median lobe. The distal margin of the median lobe has serrate setae and small spines in naupliar stages IV-VI.

TABLE 1

Mean size of cultured larval stages of M. rosa.
Abbreviations: n, sample number; TL, total length; SL, shield length; W or D, shield width or cyprid depth.

Stage	n	TL (mm)	SL (mm)	W or D (mm)
Egg	9	0.21		0.15
Nauplius I	11	0.27		0.16
Nauplius II	20	0.47		0.23
Nauplius III	15	0.53		0.29
Nauplius IV	13	0.61	0.37	0.35
Nauplius V	10	0.76	0.46	0.46
Nauplius VI	10	0.98	0.70	0.56
Cyprid	10	0.70		0.35

The diagnostic features of each larval stage can be summarised as follows:

Nauplius I (Figs 1**A**, 1**H**, 2**A**)

Body globular, but generally typical of stage I balanid larvae. Lateral shield margin smooth; dorsal thoracic spine and furcal spines smooth.

Nauplius II (Figs 1**B**, 1**I**, 2**B**, 2**G**)

Shield margin smooth, frontal filaments short, frontolateral horns of moderate length; dorsal thoracic spine barbed, longer than thoraco-abdominal process; smooth series-1 spines present.

Nauplius III (Figs 1**C**, 1**J**, 2**C**, 2**H**)

Morphologically similar to stage II except in size, but with incipient spination at tips of frontolateral horns; first rudiments of maxillae on thoraco-abdominal process; small spines medially between series-1 spines.

Nauplius IV (Figs 1**D**, 1**K**, 2**D**, 2**I**)

Shield with smooth margin; paired, smooth dorsal shield spines and posterior shield spines; frontolateral horns prominent, divided at tips; barbed dorsal thoracic

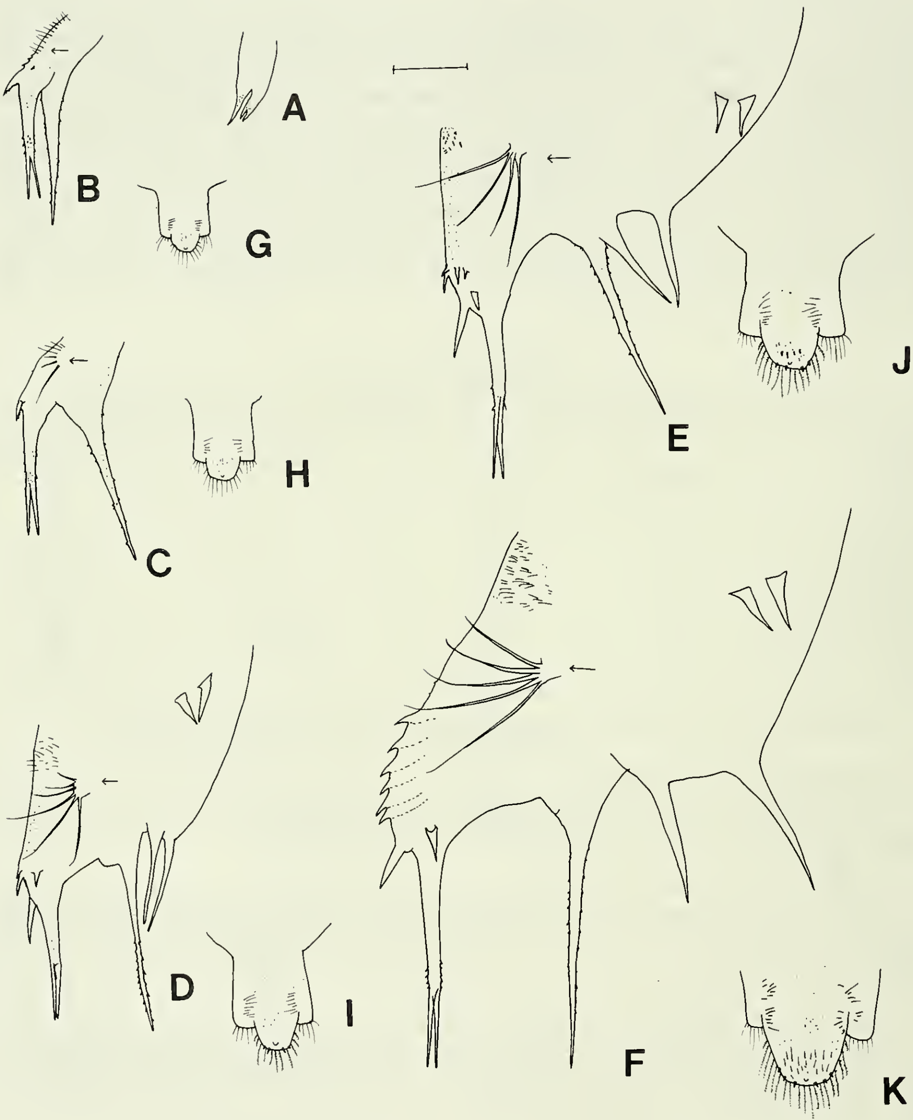

Fig. 2. Megabalanus rosa. Thoraco-abdominal process (lateral view) of naupliar stages I-VI (**A-F**); shape of labrum of naupliar stages I-VI (**G-K**). Arrow indicates position of maxilla for each naupliar stage. Scale = 0.1 mm.

spine longer than thoraco-abdominal process. Four series-2 spines anterior to long series-1 spines, arranged as paired lateral spines and two median spines in antero-posterior sequence.

Nauplius V (Figs 1**E**, 1**L**, 2**E**, 2**J**)

Morphologically similar to stage IV except in size, but with dorsal thoracic spine now equal in length to thoraco-abdominal process. Long, smooth series-1 spines flanked by a similar pair of series-3 spines; series-2 spines with an additional small pair laterally. Anterior to the series-2 spines, several rows of small spines parallel to the long axis.

Nauplius VI (Figs 1**F**, 1**M**, 2**F**, 2**K**)

Morphologically similar to stage V except in size, but with prominent frontal filaments, and series-1, 2 and 3 spines of thoraco-abdominal process in usual balanoid stage VI pattern. Developing compound eyes conspicuous in older larvae.

Cyprid (Fig 1**G**)

Fusiform, pointed anteriorly and posteriorly, sculptured externally.

Setation of the Appendages

The setal formulae of the antennules, antennae and mandibles of the six naupliar stages of *M. rosa* are given in Table 2 and illustrated in Figs 3**A**-3**F**, 4**A**-4**F** and 5**A**-5**F**. There was almost no variation in setal number among individuals at each naupliar stage. Plumodenticulate setae were present on the endopod of the antennae of stages II-VI, but not on the mandibular endopod of the same stages. A spine was found proximally on the mandibular endopod in stages II-VI.

Discussion

The egg of *Megabalanus rosa* is of greater than average size for a balanid (210 x 150 μm), but larval growth after hatching is dependent on planktotrophy in the normal balanid manner. At 20°C the duration of larval development to the cyprid is 14-16 days, yielding a cyprid of 0.70 mm average length. Larval size and mode of development in *M. rosa* thus conform to the general balanid pattern, but are at the larger end of the size range for planktotrophic larvae of this group.

On the basis of these observations, it seems likely that the development of *M. rosa* represents a generalized condition for *Megabalanus*, and that the unusual features reported by Daniel (1958) for the development of *Megabalanus tintinnabulum* are specializations. *M. tintinnabulum* has a much larger egg (300 x 130 μm), which may account for its ability to develop to the cyprid stage in 26-48 hours without feeding and to produce a large cyprid, 0.82-0.89 mm long.

Egan and Anderson (1987) showed that the three genera of megabalanines represented by *Austromegabalanus nigrescens*, *Notomegabalanus agricola* and *Megabalanus tintinnabulum* each have a distinctive pattern of larval development in respect of naupliar shield shape, marginal shield spines, dorsal shield spines, rate of development, food requirements and size of cyprid (Table 3). When the development of *Megabalanus rosa* is drawn into the comparison, these distinctions remain, in spite of the fact that *M. rosa* has a much more typical larval development than *M. tintinnabulum.* It thus becomes possible to examine, on the basis of larval data, the interrelationships of the three megabalanine genera.

The larval development of *Notomegabalanus agricola*, with an egg size and hatching size similar to those of typical *Balanus* species such as *B. amphitrite* and *B. variegatus* (Egan

TABLE 2

Setal formulae for the nauplii of M. Rosa.

Abbreviations: S, simple; P, plumose; D, plumodenticulate; C, cuspidate; G. gnathobase; sp, spine; S^p*, simple, sometimes plumose; st, setal stub.*

Naupliar stage	Antennule	Antenna		Mandible	
		Exopod	Endopod	Exopod	Endopod
I	SSSS:SS:S:S	S:4S	SSS:SS:SS:SS:G	S:S:S:S	SSS:SS:SS:SS:G
II	SSPS:SP:P:S	SP:4P:S	PPS:SP:PD:SPC:G	P:P:P:P:st	SSS:SP:PCS:spPC:G
III	S:PSPP:SP:P:S	PP:5P	PPP:SP:PD:SPCS:G	P:P:P:P:S	SSS:SPS:PCP:spPPC:G
IV	S:P:PSPP:SP:P:S	PPP:6P	PPPSS:SPS:PD:SPCP:G	P:P:P:P:S^P	SSSS:SPP:PSCP:spPCP:G
V	S:P:P:PSPP:SP:S:P:S	PPP:7PS^P	PPPSP:SPP:PD:SDCP:G	P:P:P:P:P:S	SSSS:SPSP:SPCP:spPPC:G
VI	S:P:P:PSPP:SP:P:PS:S	PPPP:8P	PPPSP:SPP:PD:SPCP:G	P:P:P:P:P:P	SSSS:SPSP:PSCP:spPCP:G

TABLE 3

Larval features of megabalanine genera

Feature	***Austromegabalanus nigrescens***	***Notomegabalanus agricola***	***Megabalanus rosa***	***Megabalanus tintinnabulum***
Feeding	Planktotrophic	Planktotrophic	Planktotrophic	Lecithotrophic
Egg diameters (mm)	0.21 x 0.11	0.15 x 0.11	0.21 x 0.15	0.30 x 0.13
Length/width ratio of nauplius	2.00-2.50	2.00	1.65-2.00	1.20-1.48
Dorsal shield shape	Elongate pentagonal	Elongate globular	Globular	Globular (fat)
Marginal spines	Prominent	Absent	Absent	Absent
Dorsal spines	2, increasing to 4	Absent	2	Absent
Stage VI shield length x width (mm)	0.44 x 0.38	0.46 x 0.38	0.98 x 0.56	0.46 x 0.42 (fat)
Cyprid, length (mm)	0.49	0.50	0.70	0.85
Rate of development	to cyprid, 13-23 days	Not known	to cyprid, 14-16 days	to cyprid, 26-48 hours

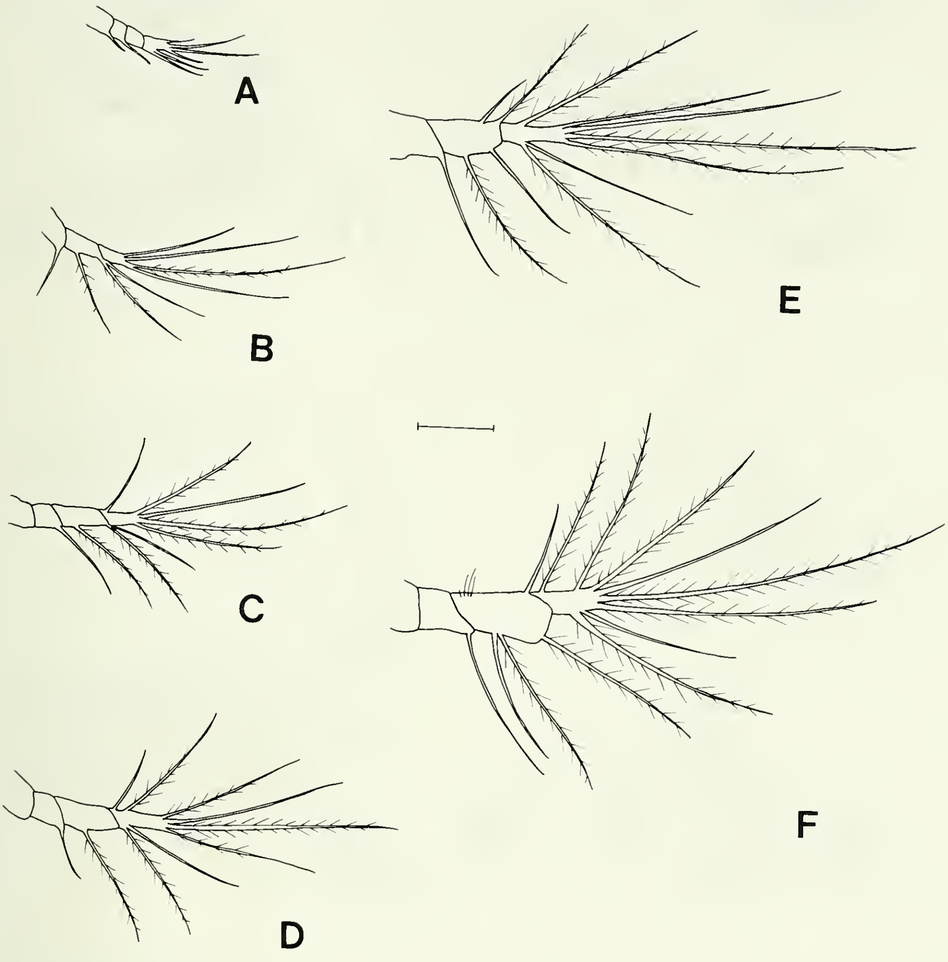

Fig. 3. Megabalanus rosa. Antennule of naupliar stages I-VI (**A-F**). Scale = 0.1 mm.

and Anderson, 1986), differs little from that of the two latter species. The development of *Austromegabalanus nigrescens*, from a larger egg, is distinctive in several ways. The nauplius, although relatively large, is long and narrow, with prominent marginal spines and four dorsal spines on the shield. The resulting cyprid, on the other hand, is no larger than that of *Balanus variegatus*. A better model for the development of *A. nigrescens* may be that of the archaeobalanid genera *Hexaminius and Conopea*, also with a spiny dorsal shield. *Megabalanus rosa*, developing from a somewhat more voluminous egg than that of *A. nigrescens*, presents a sharp contrast. The larvae are more globular, with a smooth shield margin, although they do develop a pair of dorsal shield spines. The emergent cyprid is also larger. These features are further exaggerated in the development of *Megabalanus*

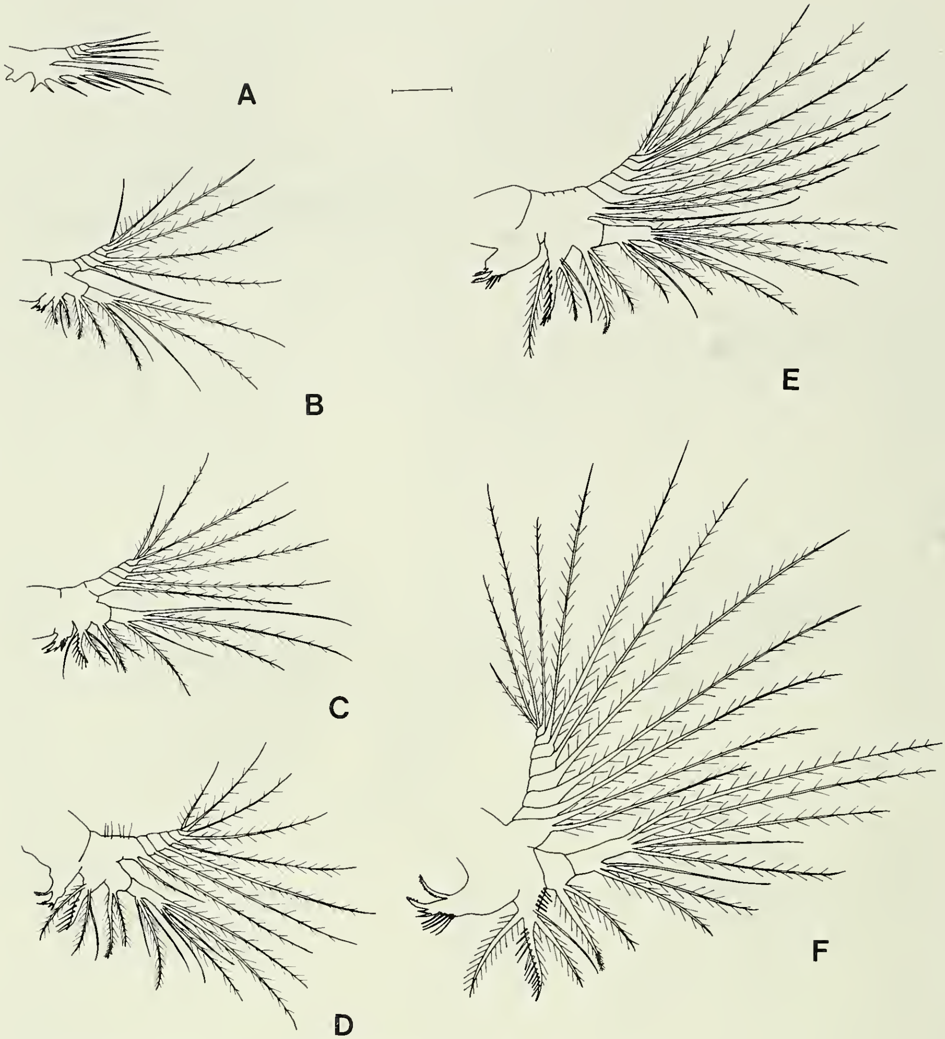

Fig. 4. Megabalanus rosa. Antenna of naupliar stages I-VI (**A-F**). Scale = 0.1 mm.

tintinnabulum, with its large egg, short, fat nauplii, smooth shield lacking dorsal spines, rapid development and large cyprid.

Recent data on sperm ultrastructure (Healy and Anderson, 1990) raised the possibility that *Megabalanus* and *Austromegabalanus* may have had separate origins. The contrasting larval developments of the two genera give further weight to this possibility. The presence of dorsal shield spines on the older nauplii of *M. rosa* seems likely to be a convergent feature, in view of the occurrence of these spines in the unrelated *Balanus venustus* and in the Lepadomorpha (Lang, 1979; Dalley, 1984; Moyse, 1987).

A detailed comparison of larval setation between the two megabalanine species for which sufficient detail is now available, *A. nigrescens* and *M. rosa*, reveals minor differences in the setation of the endopod of the antenna and mandible. The antennal endopod of *M. rosa* has an additional simple seta terminally in nauplius IV-VI. The

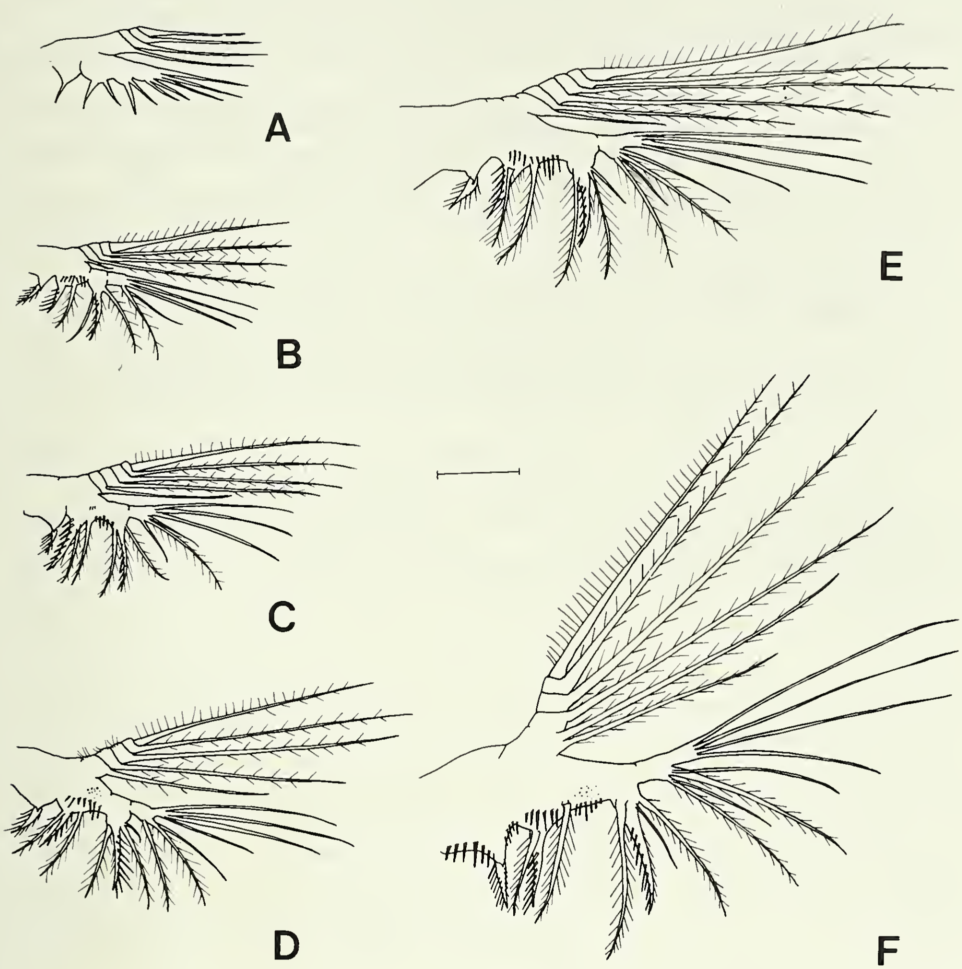

Fig. 5. Megabalanus rosa. Mandible of naupliar stages I-VI (**A-F**). Scale = 0.1 mm.

mandibular endopod of *A. nigrescens* has two plumodenticulate setae in the subterminal group, where *M. rosa* has plumose setae, and sometimes shows a similar replacement of one of the four plumose setae by a plumodenticulate seta in the next most proximal group. In the absence of knowledge of the larvae of other megabalanine species, the significance of these setal differences cannot be fully assessed.

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